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FROM STUDIES OF THE STRUCTURE OF A SPECIES OF COMMERCIAL FISH

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In spite of the vast number of investigations devoted to the /19
study of the population structure of a species in the world of fish, only a few have dealt with the question to the degree that is necessary for the development of conceptions of a species in ichthyology and for the solution of fisheries' problems. This is the situation in that area of zoology which, since the works of F. Heincke [31], is rightfully considered to be a "pioneering" area with respect to the formulation of and attempts at effectively solving the problems of the intra-species differentiation of economically important species of living organisms.

In our view, the main reason for the low level of effectiveness of investigations along these lines is that they have not been formulated in a specific direction with a clear formulation of purpose and final results, methodology and research methods. The formulation of these investigations

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in a specific direction is certainly a fairly complex problem. At the same time, there are undoubtedly preconditions for its solution, especially as vital problems of marine fishery investigations require this.

The purpose of this report is to show that investigations of the structure of a species are entirely realistic when certain conditions are observed, arising, firstly, from conceptions of a species based on the positions of the synthetic theory of evolution (as comprehended by K.M. Zavadskii [10, 11, 12]) and, secondly, from the experience of investigations of the structure of a species in ichthyology.

TWO POSITIONS IN CONTEMPORARY CONCEPTIONS OF THE STRUCTURE OF A SPECIES IN THE WORLD OF FISH

As we know, F. Heincke, in ascertaining whether the herring of the North Atlantic consists of one large homogeneous stock or several stocks, arrived at the conclusion that the stock was heterogeneous and was represented by several forms of herring. These forms are characterized by certain morphological differences /20 and can only be found in certain regions. Heincke called the characteristics by which they differ "race marks" and the established forms themselves "races". He defined a race as a spawning community whose members occur in a state of reproductive mixture and differ from other communities by certain morphological characteristics which are transmitted by heredity [31].

We draw attention to two factors, which will later become a subject of discussion. Firstly, by emphasizing the hereditary nature of the differentiating characteristics, F. Heincke indirectly expresses his conviction that the "races" isolated by him are self-reproducing and are stable in time. This will have great importance in a subsequent discussion, although the thesis of the hereditary nature of the characteristics used by him will later be criticized with good reason. Secondly, the meaning Heincke gives the term "race" quite clearly

indicates reproductive homogeneity, i.e. the further indivisibility of the race as a unit of a species. Such an understanding of a "race" is in keeping with the often cited conception of this category by the ichthyologist G. Krefft [34]: "...undoubtedly, the term "race" in zoology can only be used to designate intraspecific genetically homogeneous units within a species or within a racial circle of morphologically or physiologically separate units. At the same time, it must be emphasized that geographic races in limited ranges from transitional forms, which emerge as a result of bastardization". Even earlier, V.S. Kirpichnikov wrote the following: "We consider races to be the smallest possible populations which essentially do not mix with other populations. Completely free reproduction is generally possible only within each race, and if there is considerable mixing during reproduction, the differences between races are not sufficiently permanent" [15, p. 181].

Thus, the conceptions that species of fish are formed by races that are 1) self-reproducing and stable in time and 2) indivisible units of a species became the starting point as research into the structure of a species in ichthyology unfolded.

This line of thought, which was initiated in the works of G. Heincke and his followers [24, 35, 35], was subsequently developed by L.S. Berg with respect to diadromous fish in his work "Vernal and Hiemel Diadromous Fish" [3]. The author provides a fairly good argument in defence of the point of view that under natural conditions different seasonal races of salmonid and sturgeon fish cannot change from one into the other because of the different ecology of spawning, although /21 "... we have no basis for insisting on the hereditary nature of spring and autumn races of salmon" [3].

A.N. Derzhavin [9] called the works of N.L. Gerbil'skii [4,5] and V.Z. Trusov [25] on the separation of three biotypes of sturgeon (intraspecific biological groups), differing in biological development, a new basis for the theory

of vernal and hiemal races. Underlining the continuity with the study of vernal and hiemal forms by L.S. Berg, N.L. Gerbil'skii [7] examined biological groups as hereditarily more or less stable and together with this qualitatively different biologically. Biological groups of sturgeon became the subject of serious discussion, which essentially reflected the differences of opinion concerning specific forms of existence of a species in nature. N.L. Gerbil'skii answered extremely convincingly the principal question of his opponents, as to whether one biological group changes into another or is constant: "These groups really exist in nature, they possess different biological properties and require a different piscicultural approach", and later, "...in contrast to Atlantic salmon, many biological groups of sturgeon are more isolated (for example, in spawning time) and, therefore, crossings are unlikely; such intraspecies biological groups are genetically more stable" [6]. The reference to a different piscicultural approach merits special attention as a practical verification of the properties of different biological groups.

Thus, in ichthyology, the view has developed, over quite a long time, based on different fish, that fish species in nature are represented by self-reproducing elementary units - "races" according to F. Heincke, "seasonal races" according to L.S. Berg, and "biological groups" according to N.L. Gerbil'skii.

Another viewpoint was expressed in domestic ichthyology as early as the beginning of the 50's, as an alternative to the views of L.S. Berg, and particularly N.L. Gerbil'skii. In summarizing the main factors of the criticism of the views of L.S. Berg and N.L. Gerbil'skii, A.N. Derzhavin writes: "...The different qualitative nature of 'biological groups' according to N.L. Gerbil'skii creates biologically isolating mechanisms - a seasonal and physiological isolation of groups, which excludes the possibility of crossing and thereby decreases the potential possibilities of a species. If a similar situation were to exist in nature, it would

indicate the presence of a process of degradation of sturgeon species" [9, p. 270].

The opinion of A.N. Derzhavin was by no means particularly significant. It was essentially the position that was subsequently expressed by G.V. Nikol'skii [20, 21] and his followers (L.Ye. Anokhina [1], G.D. Polyakov [22], Yu.Ye. Lapin [17, 18] and others). The essence of these views was clearly defined by K.M. Zavadskii and A.S. Mamzin [13]. We are talking about the neo-Lamarckian /22
understanding of evolution, associated with the search for sources of development in conflict in the "organism - environment" system, and the adoption of the individual as the elementary unit of evolution of an organism [21, p. 133]. According to this point of view, only the species and individual are real. The species is understood to be a self-reproducing grouping of individuals [21, p. 13], and individuals possess characteristics which are specific to the species and reflect the nature of its interaction with the environment. The scope of variation of organisms can change with adaptation. And further: "Any species characteristic, any species property, including the scope of individual variation, and inherited and non-inherited properties... In this sense, all characteristics and properties of intra-species groupings which emerge as adaptations to the environment are inherited and simultaneously non-inherited..." [21, p. 57].

Continuing this thought of G.V Nikol'skii, Yu.Ye. Lapin writes: "Intra-species groupings are invertible, changing over from one to the other, although generatively relatively separate, and the degree of generative isolation increases from seasonal races to geographic races - sub-species" [18, p. 57]. The logical (and simultaneously, applied) conclusion to these views were the conclusions of L.Ye. Anokhina [1] concerning the dynamic nature of seasonal races of Baltic-Sea herring (the possibilities of changing from one to the other). In due course, we expressed our position with respect to her views [2]. The denial of the role of intra-species groupings as concrete forms of life of a species,

however paradoxical this is, was heard at the same time as the positions of the synthetic theory of evolution (as understood by E. Mayr [19], K.M. Zavadskii [10] et al.) began being successfully realized in zoology, ornithology, entomology and botany. It was primarily a question of corroborating the notion of a population as a concrete form of existence of a species in nature and an elementary unit of evolution.

An analysis of the structure of a species from the positions of the synthetic theory of evolution was first fairly clearly heard in the work of J. Blexter, "The Racial Problem in Herring in Light of Contemporary Physiological, Evolutionary and Genetical Theory" [27]. For a number of reasons this work did not give a complete picture of the structure of the species of Northeastern-Atlantic herring. At the same time, it finally defined the line of thought and methodology of studying the structure of a species in the world of fish which represents the only promising solution to this problem. J. Blexter started from E. Mayr's conception of a species [27] - "A species is a group of actually or potentially cross-breeding natural populations which is reproductively isolated from other such groups".

One can argue about the degree of perfection of such a definition of a species; however, its essence - that a species in nature exists in populations - remains unchanged. The specific characteristic of Blexter's research was that /23 the study of the population structure of the species of herring was not his objective. He dealt with a broader task, that of defining the nature and degree of difference between spring-spawning and autumn-spawning herring, and he solved the problem by showing that differences on a biological basis (differences in the spawning season) can be determined by the relationship between herring with different spawning seasons at the level of duplicate species. Recently, clear genetic and biochemical differences have been shown between

Northeastern-Atlantic herring with different spawning seasons by I. Kornfield et al [33].

Having introduced a neo-Darwinian way of thinking and methodology into the practice of studying the structure of a species in the world of fish J. Blexter went up to the structure of a biological ("population") species. However, he did not take the matter to the population structure. The Soviet ichthyologist, E.A. Oyaveer [38] did this for Baltic herring with autumn and spring spawning.

From the foregoing, it is obvious that there are two alternative variants of the study of the structure of a species. The first, emanating from the principles of the synthetic theory of evolution, proceeds from the notion of a species as a stage in the evolution of a group of organisms, characterized by closure of the genetic system, and of populations as a concrete form of existence of a species in nature. The second, arising from the neo-Lamarckian understanding of evolution, treats a species as a self-reproducing grouping of individuals, and intra-species groupings (including populations) as relatively separate generatively, however crossing over mutually. It is not difficult to see that only the first understanding of species and population provides the basis for the knowledge and practical utilization of populations of living organisms. The second point of view actually excludes the population as an element of the structure of a species: endowed by authors with the ability to change infinitely, depending on the changes in the environment, a population in the neo-Lamarckian sense virtually has no limits, i.e. it in fact has no concrete content. Because of this, it is unacceptable either from a theoretical or practical point of view.

To understand the essence of the two positions with respect to the question of the structure of a species is to understand the essence of the problem of intra-species differentiation and to see ways to resolve it for specific species.

Our analysis of these positions was fairly detailed because an investigator who has no conception of them is not only incapable of dealing with the question of the structure of a species satisfactorily, but on the contrary is capable of introducing additional confusion to this already fairly complicated problem.

HOW TO STUDY THE STRUCTURE OF A SPECIES IN THE WORLD OF FISH EFFECTIVELY

To study the structure of a species means to identify its populations in such a way so that the conclusion about them is verifiable by research methods and the practical operation of the fishing fleet and does not contradict the contemporary conceptions of a species.

We admit that different investigators can variously present ways of resolving the question of the structure of a species. The essence of our aproach can be reduced to the following. The principal way of identifying natural populations stems from the definitions of a population which in our opinion are most correct, particularly the definition by K.M. Zavadskii: "... a local population is the main and elementary form of adaptation and existence of a species, and the smallest structural unit of its stock capable of more or less independent reproduction and development [10, p. 32]. K.M. Zavadskii understood a "local population" to be a population in the contemporary sense of the word (earlier, the entire stock of a species was called a population). From this definition it is clear that the general distinguishing feature of a population is the capacity for more or less independent reproduction and development. Disregarding development as a criterion, which is inaccessible to analysis, we obtain only a criterion such as self-reproduction. Adaptations associated with self-reproduction are numerous. Therefore, the greater the number of parameters studied, associated with reproduction (in the broad sense), the greater the probability of a successful identification of populations.

The practice of studying the population structure of the herring of the NE Atlantic, the sardinella of the Central-East Atlantic, and other species of fish confirmed the effectiveness of the use of the following parameters - the size and age at which sexual maturity is attained, the average size and age of a spawning contingent, the size and age limits of mature fish, the periods and times of reproduction, individual and population fecundity, etc. [16, 7, 30]. What is the principal "novelty" of these generally traditional parameters in ichthyological investigations? The fact is that the successive adoption of population conceptions postulated by the synthetic theories of evolution requires adoption of the theses that 1) "... ontogenesis is a rigorously determined type of development, based on solid historically assigned programs and representing the decoding of them under concrete conditions" (according to K.M. Zavadskii and A.S. Mamzin [13]), and 2) noting the physiological nature of the parameters listed above, it should be borne in mind that physiological criteria can play an important role as taxonomic characteristics (from V.S. Ivlev [14]). Hence, it follows that physiological characteristics are /25 determined, and they are specific "... for lower, mainly intraspecies subdivisions of fish", as noted in the work of V.S. Ivlev which is cited above.

Populations are physiologically specific - this is what appears in the foreground. This was well illustrated by A.S. Danilevskii [8] on insects. L.I. Khozatskii [26] showed theoretically what role the formation of distinctive physiological characteristics plays in the formation of varieties. His point of view is all the more interesting since G. Krefft et al. (cited above) came forward at the same time rejecting the role of the physiological factor in the formation of a subspecies: "... hitherto, the formation of a subspecies on no account was considered to be proven only on the basis of the specific nature of the reproduction period..." [34, p. 145].

Speaking of the possibilities of using the given characteristics in

population investigations, it should be particularly emphasized that the work on commercial "densities" provides exceptional data, making it possible, firstly, to have a vast amount of statistics, and, secondly, by means of regulating the collection of data, to acquire data on the frequency of the values of determined parameters in presumed populations. In essence, this is a practical verification of the hypothesis of the population composition of a commercial species.

The functional differences which are manifested in the non-conformity in time of cyclical manifestations, associated with feeding migration or reproduction, deserves special attention. K. Lucas is well aware of this when he says "... it must be understood that the absence... of morphological, physiological and other differences does not necessarily mean that two groups of fish are permanently connected as a result of mixing or the exchange of individuals. Each of them can be absolutely individual" [37, p. 273].

In conclusion, it is necessary to emphasize the role played by the determination of the specific qualitative nature of the range of tentative populations in the understanding of the population structure of a species. Few authors directed their attention to this [7, 38, 32] although it is the logical development of the thesis that a population is a unit of a biocoenosis and development takes place by means of resolving the contradiction in the "population - environment" system. The specific qualitative nature of the environment should correspond to the specific qualitative nature of the population (if we are speaking of allopatric populations). In the case of sympatric populations, it is necessary to understand what is the distinctive feature of the determination of the differences in the vital activity of coexisting populations by means of one and the same values of environmental factors.

We did not concentrate attention specifically on the possibilities of

other approaches (morphological, geographic, ecological, genetic, etc.) in dealing with the question of the structure of a species, including population structure. In due course, they were sufficiently thoroughly discussed by /26 K.M. Zavadskii [10]. As to the applicability to fish, this was discussed at a Special Conference on the Problems of Herring Races [29] and in a number of other studies. We shall only note that it is most difficult for investigators to part with their conviction of the "omnipotence" of a comparative analysis of mophological and meristic characteristics. A number of papers in this collection testify to this. The validity of these characteristics have in fact been questioned since the time of F.N. Heincke (see J. Blexter's brief survey [27]). In this regard, I.F. Pravdin wrote: "In the study of fish races, morphological characteristics and differences must be examined in parallel with biological characteristics: no doubt there are races which differ more biologically than somatically among themselves" [23, p. 159].

The authors of studies along these lines try not to focus attention on 1) the unknown nature of differences found in certain cases, and 2) the modifying effect of the conditions of development.

A subject of special discussion is the genetic analysis of the structure of a species. Our attitude to it was determined by such "touchstones" as the seasonal races of herring. A work was cited above by I. Kornfield et al. [33] which showed for the first time the genetic differences between the seasonal races of herring in the NW Altantic. It is the view of the authors that the method does not reveal population differences.

CONCLUDING COMMENTS

The study of the structure of a species in ichthyology in our country has developed in conditions of fundamentally different notions of the essence of the problem.

The notion of species and populations from the point of view of contemporary Darwinism was opposed to the notion based on the neo-Lamarckian understanding of a species. The latter virtually excluded the position of the reality and discrete (or relatively discrete) nature of populations together with all the conclusions arising from this. From the point of view of marine fisheries research, both the object of fisheries and the object of research "disappeared". Only researchers who perceive the basic problems of marine fisheries and the scientific methods of solving them in an extremely formal way could fail to note this.

The main condition for a successful solution to the question of population structure in the world of fish is to recognize, not on the basis of the form, but on the basis of the essence of the reality of natural populations, the capacity of populations for stable existence as a result of self-reproduction, the physiological or functional nature of the differences between the populations of a species, and the reality of the oceanological factors of isolation.

CONCLUSIONS

1. The main condition for productive research on the structure of a species is the guiding principal of contemporary conceptions of a species and the forms of its existence.

2. One of the concrete ways of arriving at a practical solution to the question of the population structure of a species is by means of an ecological and physiological analysis of the parameters which determine the specific nature of hypothetical populations.

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